PHYLOGENETIC RELATIONSHIPS AND TAXONOMIC STATUS OF THE PALEOENDEMIC FAGACEAE OF WESTERN NORTH AMERICA: RECOGNITION OF A NEW GENUS, *NOTHOLITHOCARPUS*

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Abstract

We investigated the phylogenetic relationships and taxonomic status of the castaneoid component (*Lithocarpus* and *Chrysolepis*) of the family Fagaceae that is endemic to the California Floristic Province (CA-FP). Over 7800 basepairs of nuclear and chloroplast DNA were analyzed in 17 taxa representing the breadth of phylogenetic diversity in the family. The genus *Lithocarpus*, as currently defined, is clearly polyphyletic due to the inclusion of *L. densiflorus*. Here, we designate this taxon as a new genus, *Notholithocarpus*, which can be recognized morphologically by its relatively small, subprolate pollen. *Notholithocarpus* is more closely related to *Quercus*, *Castanea*, and *Castanopsis*; *Chrysolepis* was resolved as the sister group to *Lithocarpus* sensu stricto. These results indicate that *Notholithocarpus* does not possess true 'flower cupules,' which define *Lithocarpus* sensu stricto, but like the oaks, the single flower per cupule is derived through the abortion of lateral flowers within each cupule. Further study is required to confirm this characteristic. A formal taxonomic treatment is presented with new combinations.

Key Words: California Floristic Province, *Chrysolepis*, Fagaceae, *Lithocarpus*, *Notholithocarpus*, phylogeny, sudden oak death, tanbark oak.

The California Floristic Province (CA-FP) of western North America is rich in paleoendemic plant species that highlight the botanical legacy of the region and stimulate discussion on the affinities of many of these putatively isolated taxa (Stebbins and Major 1965; Raven and Axelrod 1978). Among these taxa are representatives of the largely tropical East Asian castaneoid subfamily of the Fagaceae: *Chrysolepis* Hjelmq. and *Lithocarpus* Blume. Both are morphologically similar to other broadleaf evergreen Fagaceae of eastern Asia, but their phylogenetic position within Fagaceae is either unresolved or has been put into question with recently available data. In this study, we address the relationships of the castaneoids of the CA-FP and discuss the implications of our findings in the context of taxonomy, cupule evolution, and biogeography.

The two castaneoid taxa in question are well represented in several CA-FP communities (Barbour and Minnich 2000), and both express sufficient differentiation in habit and leaf morphology for the recognition of taxa at the subspecific- to species-level. The tanbark oak, *Lithocarpus densi-flora* var. *densiflorus* (Hook. & Arn.) Rehder, a tree that reaches 45 m, often occurs as a co-dominant in the redwood and mixed evergreen forests of the north coast ranges; its shrub form, *L. densiflorus* var. *echinoides* (R. Br. ter) Abrams is more common in open conifer forests and dry slopes of the northern interior CA-FP at higher elevations. The giant chinquapin, *Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmq., a tree potentially reaching 50 m, also occurs mostly in redwood and mixed evergreen forest. The bush chinquapin, *Chrysolepis sempervirens* (Kell.) Hjelmq., is more common at higher elevations as a low-growing shrub on rocky slopes under coniferous forests of the Sierra Nevada and in the isolated interior ranges of southern California.

Taxonomic delimitation of the castaneoid genera is based largely on characters of the pistillate flower and cupule. The most important morphological characteristic for defining *Chryso-lepis* is a cupule with internal valves separating the fruits (Hjelmquist 1948). This condition is autapomorphic within Fagaceae, and the valves have been interpreted as vestiges of the branches

of higher-order inflorescences (Nixon and Crepet 1989). Both chinquapin species originally were treated in the chestnut genus *Castanea* Miller, and later transferred to the strictly Asian genus *Castanopsis* (D. Don) Spach, consistent with their evergreen habit, leaf venation, and spiny cupule. Hjelmquist's (1948) segregation of the chinquapins into *Chrysolepis* was supported by Jones' (1986) foliar investigation of the family. He noted that compared to *Castanopsis*, *Chrysolepis* has smaller leaves and unique thick-walled peltate trichomes, likely adaptations to xeric conditions. Recent phylogenetic studies also have supported this distinction, resolving *Castanea* and *Castanopsis* as sister genera to the exclusion of *Chrysolepis* (e.g., Manos et al. 2001; Oh and Manos 2008).

The taxonomic history of *Lithocarpus densiflorus* is relatively straightforward. The species was recognized first within *Quercus*, with the following commentary: "This remarkable plant has very much the appearance of a *Castanea*, the fruit in the only specimen we possess being situated at the base of a male somewhat fascicled catkin of the former year, while the numerous male catkins of the present year present no appearance whatever of female flowers." (Hooker and Arnott 1840, p. 391). The acorn-like fruit of *L. densiflorus* develops biennially from a single pistillate flower surrounded by a valveless cupule. Miquel (1857) first introduced *Quercus* subg. *Pasania* in a treatment of south Asian species of Fagaceae and Örsted (1866) later raised the subgenus *Pasania* to the generic rank, wherein *Pasania densiflora* (Hook. & Arn.) Oerst. was treated together with a mixture of largely Asian species under subg. *Eupasania*. Although no type has been associated with the name *Pasania*, the name is often misapplied to Asian species of *Lithocarpus* (Prantl 1888). Rehder (1917) treated *Pasania densiflora* within *Lithocarpus*, and Camus (1936–1954) placed *L. densiflorus* within *Lithocarpus* subg. *Pasania*, in the monotypic sect. *Androgyne*.

Historically, there has been little doubt about the relationship of *L. densiflorus* to the approximately 250 species of Asian *Lithocarpus* (stone oaks). The genus concept is supported by the flower-cupule described by Forman (1966a, b), wherein each pistillate flower of a dichasium is surrounded by a distinct valveless cupule. As a whole, the genus *Lithocarpus* shows abundant variation in inflorescence structure, sexual condition of the flower spikes, numbers of staminate and pistillate flowers in each dichasium, fruit type, and cupule type and ornamentation (Kaul 1987; Cannon and Manos 2001). In *L. densiflorus*, the inflorescences may be androgynous with pistillate flowers at the base, or entirely staminate. There is a single pistillate flower per dichasium, and the cupules bear strongly reflexed scales.

While the combination of reproductive features observed in *L. densiflorus* fits comfortably into the range of variation observed in Asian *Lithocarpus*, non-floral studies have suggested otherwise. Most Asian *Lithocarpus* possess 2 to 4-rayed thick-walled trichomes, while *L. densiflorus* has distinct multiradiate thin-walled trichomes (Jones 1986; Cannon and Manos 2000). In addition, previous molecular phylogenetic studies showed that *L. densiflorus* does not form a clade with species of Asian *Lithocarpus*, one of the most strongly supported groups in all of Fagaceae (Manos et al. 2001); the placement of tanbark oak remained largely unresolved in that analysis.

In this study, we clarify these lingering questions about the phylogenetic relationships among the castaneoid taxa of the Fagaceae, particularly in relation to the endemic CA-FP taxa. Our analysis involves three main goals: 1) phylogenetic reconstruction of a broad sampling of Fagaceae, representing all major lineages, using multiple DNA sequence data sets; 2) analysis of pollen morphology of *L. densiflorus* to further elucidate its relationship to Asian *Lithocarpus*; and 3) taxonomic revision of *L. densiflorus* based upon these results.

Materials and Methods

Molecular phylogenetics

Seventeen taxa representing all of the currently recognized genera and major lineages of Fagaceae were chosen for study based on previous phylogenetic analyses (Manos and Stanford 2001; Manos et al. 2001; Oh and Manos 2008). Previous analyses addressed intra- and interspecific sampling of the castaneoids of the CA-FP, as well as *Lithocarpus* and *Castanopsis*. The current sample is designed to focus on the broader relationships within Fagaceae using more data. The names, authorities, sources, geographic origin, and GenBank accession numbers are summarized in Appendix I. The genus *Fagus* is consistently recognized as sister to all remaining Fagaceae; it is used here as the outgroup (Manos and Steele 1997; Li et al. 2004).

We included two nuclear loci (ITS region and *CRABS CLAW* or *CRC*) and three chloroplast regions (*trnK-matK/trnK*, *atpB-rbcL* and *ndhF*). The *CRC* data were taken from Oh and Manos (2008) and the nuclear ITS and chloroplast *trnK/matK* and *atpB-rbcL* data were obtained from Manos and Stanford (2001) and Manos et al. (2001). Some sequences of the *trnK/matK* region and most of *atpB-rbcL* sequences were newly generated here, using the methods described in Manos and Steele (1997) and Manos and Stanford (2001). The *ndhF* region was newly sequenced in this study, using the PCR primers ndhF972 (5'- ATG TCT CAA TTG GGT TAT

TABLE 1.   SPECIMENS USED IN THE POLLEN STUDY.

Notholithocarpus densiflorus, California, Butte Co., border of ponderosa pine, Douglas fir forest, 5 mi S of Sterling City, 12 Jul 1968, *Terrell s.n.* (US); Humboldt Co., Seely Ranch, ca. 2 mi E of Willow Creek on the Trinity River, 3 Jul 1971, *Stone 3034* (DUKE); Mendocino Co., along Red Mt. road, N slope of ridge SE of Red Mt., 8 Jul 1970, *Clausen 70-91* (NY); Oregon, Curry Co., Babyfoot Lake on the upper drainage of the Chetco River, 22 Sep 1964, *Chambers 2277* (US)

Chrysolepis chrysophylla, California, Shasta Co., E-face of Crater Peak, 8200 ft, volcanic, subalpine, 16 Aug 1964, *I. Olmsted 259* (DUKE).

Lithocarpus dealbatus (Hook.f & Thomson ex Miq.) Rehder; China, Sichuan, Yong-Jia: *Manos 1288* (DUKE)

Castanopsis indica (Roxb. ex Lindley) A. DC: China, Yunnan, Menglum: *Manos and Zhou 1426* (DUKE)

ATG ATG; Olmstead and Sweere 1994) and FndhF2110R (5′- CCT CCT ATA TAT TTG ATA CCC TCT CC) with Phusion High-Fidelity DNA polymerase (New England Biolabs, Ipswich, Massachusetts, USA) under the following conditions in 25 μL reactions: initial denaturation at 98°C for 1 min 30 s, 40 cycles of 98°C for 10 s, 60°C for 30 s, and 72°C for 1 min, followed by final extension at 72°C for 7 min. PCR products were purified with the QIAquick PCR Purification kit (Qiagen, Valencia, California, USA). All sequences were determined at the DNA sequencing facility at the Duke Institute for Genome Sciences and Policy that uses a 3730xl DNA Analyzer (Applied Biosystems, Foster City, California, USA). Sequences were edited in Sequencher version 4.5 (Gene Codes Corporation, Ann Arbor, Michigan).

Sequences were manually aligned using MacClade version 4.06 (Maddison and Maddison 2000). Phylogenetic analysis of the combined data was conducted with maximum parsimony (MP) and maximum likelihood (ML) methods. Eighteen sites in intron four of *CRC* were excluded in the analyses because of alignment ambiguity. All other characters were treated as unordered and equally weighted in the MP analyses. Gaps resulting from multiple alignment of indels were treated as missing data. In both MP and ML analyses, heuristic searches in PAUP* (Swofford 2002) were used to find the best scored tree with 100 replicates of random taxon addition and tree bisection-reconnection (TBR) branch swapping, saving all of the best trees at each step (MulTrees). Branches with a minimum length of zero were collapsed using "amb-" option during the searches in the MP analysis (Nixon and Carpenter 1996). Bootstrap analysis (Felsenstein 1985) using the MP criterion with 500 pseudoreplicates was conducted with simple sequence addition and TBR branch swapping in PAUP*. The best fitting evolutionary model in the ML analysis was determined by the hierarchical likelihood ratio test using Modeltest 3.06 (Posada and Crandall 1998).

ML bootstrap analyses were conducted with 500 pseudoreplicates by using the program GARLI version 0.951 (Zwickl 2006). A six-substitution parameter model was employed to calculate a likelihood value. Empirical base frequencies were used, and other parameters, including the shape parameter of gamma distribution and proportion of invariable sites, were estimated from the data. Default values were used for genetic algorithm and other settings.

We tested the monophyly of *Lithocarpus*, including *L. densiflorus*, using the Shimodaira-Hasegawa test (Shimodaira and Hasegawa 1999; SH test), as implemented in PAUP*. For the SH test, MP trees generated enforcing the topological constraint were evaluated against the original MP tree based on 10,000 bootstrap pseudoreplicates using the re-estimated log likelihood (RELL) method.

Palynology

The pollen of four specimens of *Lithocarpus densiflorus* collected in California and Oregon was examined, in addition to representative species of other castaneoid genera (Table 1). Pollen grains were acetolyzed using the method in Faegri and Iversen (1950). Specimens were mounted on stubs, coated with gold palladium with a Hummer 6.2 sputter coater (Anatech), and observed and photographed using a Philips XL30 ESEM TMP (FEI Company) in the Department of Biology SEM facility of Duke University. We also measured polar and equatorial diameter and calculated the P/E ratio for 30 pollen grains of *L. densiflorus* with light microscopy (LM) using the following collections: *Terrell s.n.* (US), *Clausen 70-91* (NY), and *Chambers 2277* (US). The pollen was mounted and stained with lactophenol-cotton blue and viewed under a Leitz microscope at 1000× magnification.

RESULTS

The final alignment of combined data included 7866 characters of which 1022 were parsimony-informative. The alignment was deposited in TreeBASE (URL: http://www.treebase.org/). The MP analysis produced a single tree with a length of 1946 steps, consistency index of 0.573 (excluding uninformative characters), and retention index of 0.643. ModelTest selected the general time-reversal model (GTR; Swofford et al. 1996) with six rate parameters, the gamma distribution parameter (Γ), $\alpha = 0.793$, and proportion of invariable sites (Pinvar) = 0.4386
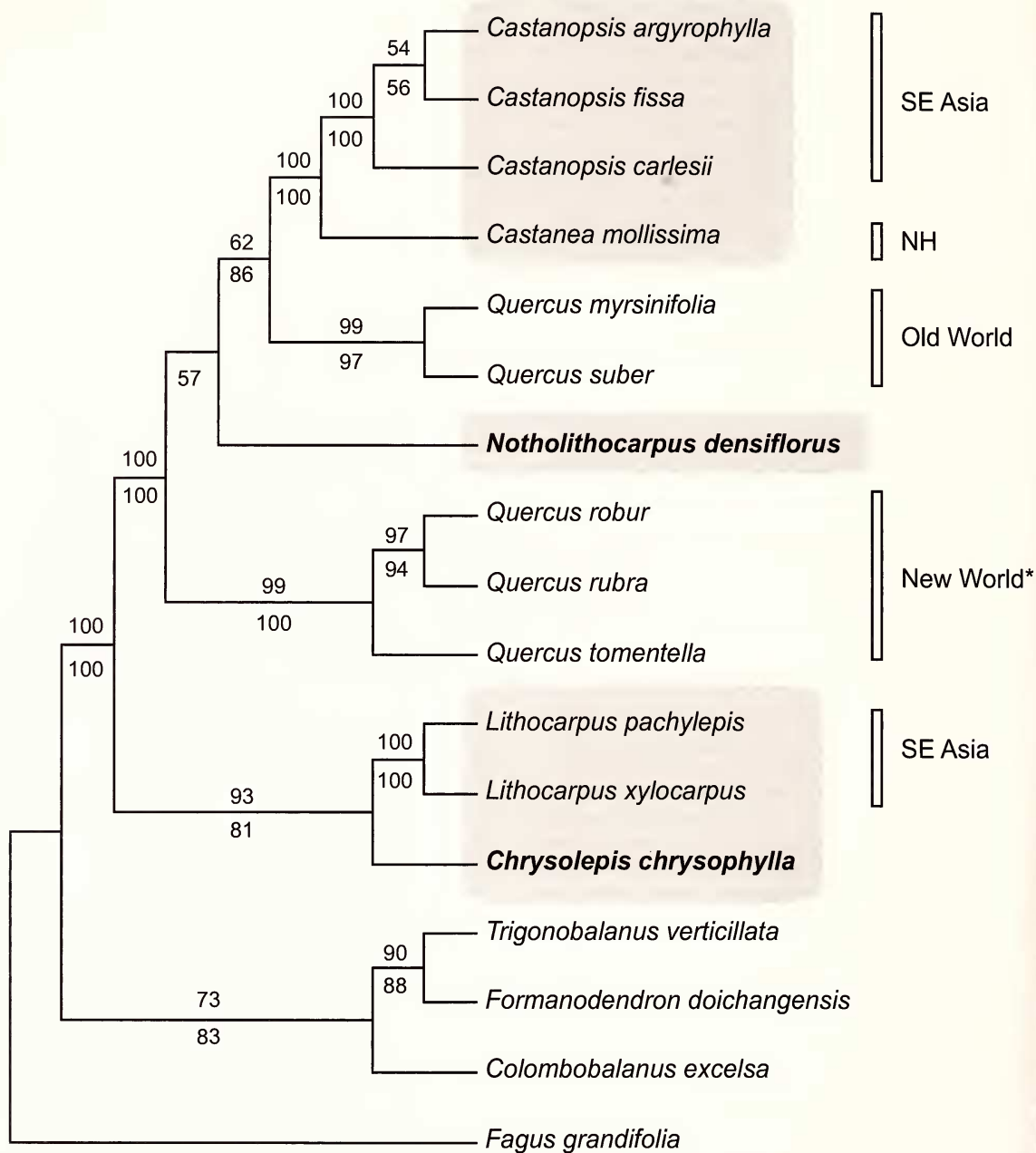
FIG. 1. Maximum likelihood tree from the analysis of the combined ITS, *CRC*, and cpDNA data. Bootstrap proportions using MP are indicated above branches and those based on ML are below. Boldfaced taxa are paleoendemics of the California Floristic Province; shaded boxes indicate subfamily Castaneoideae; area designations: SE Asia = Southeast Asia, NH = Northern Hemisphere; *New World *Quercus* clade contains approximately 15 species of Eurasian white oaks (*Quercus* sect. *Quercus* s. s.).

as the best fitting model for the data. The ML tree (Fig. 1) is identical to the MP tree, except for the position of *Lithocarpus densiflorus*. In the ML tree, *L. densiflorus* was sister to a weakly supported clade that contains Old World oaks, *Castanea*, and *Castanopsis*. In MP tree, *L. densiflorus* was placed as sister to the New World

oaks, but this relationship was not supported in bootstrap analysis (results not shown). Overall, close relationship of *L. densiflorus* to *Quercus*, *Castanea*, and *Castanopsis* was strongly supported (100% bootstrap value) in both MP and ML analyses (Fig. 1). Asian species of *Lithocarpus* formed a strongly supported clade with *Chryso-*

lepis. Forcing the monophyly of *Lithocarpus* and *L. densiflorus* required 48 additions steps, and the SH test indicated that the constrained topology is significantly worse than the original tree (P < 0.0001).

The pollen of *Lithocarpus densiflorus* is tricolporate and subprolate (Fig. 2A) with an irregularly striate to smooth exine (Fig. 2B). On the basis of examining 30 pollen grains under LM, the average measurement was 17.8 × 12.7 μm (polar = 17.2 μm, minimum and 18.8 μm maximum; equatorial = 9.42 μm, minimum and 14.1 μm maximum), and the average P/E ratio was 1.4. The pollen was smaller under the SEM (12.5 × 10.4 μm), but the P/E ratio under both conditions was similar (1.4 in light vs. 1.2 in SEM). Apparently, the pollen grains increased slightly in size after the initial preparation for LM because of fluid uptake. The pollen grains of other representative castaneoids were prolate (Fig. 2C–H): *Chrysolepis* (P/E = 1.8), Asian *Lithocarpus* (P/E = 1.6), and *Castanopsis* (P/E = 1.5).

DISCUSSION

Phylogenetic analysis of over 7800 nucleotides resolves the placement of the castaneoids of the CA-FP into two distinct lineages of the emerging phylogeny of Fagaceae (Fig. 1). *Chrysolepis* is strongly supported as sister to Asian *Lithocarpus*; while *Lithocarpus densiflorus*, hereafter referred to as *Notholithocarpus densiflorus* (formal taxonomic treatment is provided below) is placed within the *Quercus* and *Castanea* + *Castanopsis* clade, several nodes away from *Lithocarpus* s. s. These results clearly indicate the polyphyly of *Lithocarpus* s. l. A similar topology with high bootstrap support resulted from analysis of nuclear sequences (*CRABS CLAW*; ITS) with a larger sample of taxa (Oh and Manos 2008) and a previous analysis of only the ITS region across Fagaceae, including over 50 species of *Lithocarpus* s.s. also provided strong support for the monophyly *Lithocarpus* s.s., but no close relationship to *Notholithocarpus* (Manos et al. 2001).

Pollen morphology and ultrastructure have provided important systematic data to classify modern Fagaceae, as well as to assess the affinities of fossil taxa (Crepet and Daghlian 1980; Crepet and Nixon 1989b; Nixon and Crepet 1989). The pollen of *Quercus* and the castaneoid genera are diagnostic in shape and exine sculpture. The pollen grains of *Quercus* are relatively large (27.5 × 25.4 μm), subspheroidal, with a granular exine; the grains of the castaneoid genera are smaller (18.0 × 10 μm), prolate, with a smooth to striate exine (Crepet and Daghlian 1980). Pollen variation among and within the castaneoid genera is mostly limited to size, but with a trend from more prolate grains in *Chrysolepis*, *Castanea*, and *Lithocarpus* s. s., to less prolate in *Castanopsis*

(Crepet and Daghlian 1980; Wang and Chang 1989; Fig. 2). In contrast, the pollen of *Notholithocarpus* is distinctly smaller and rounder than the grains of *Lithocarpus* s.s. (mean P/E ratio of 1.68), and appears to be among the smallest and most spheroidal grains (P/E ratio of 1.2) thus far observed among extant castaneoid species (Fig. 2). In summary, we consider the distinct subprolate shape of the pollen grains of *Notholithocarpus* combined with its unique multiradiate leaf trichomes not found in *Lithocarpus* s.s. (Jones 1986) and its phylogenetic placement to be strong evidence to recognize this paleoendemic of the CA-FP as a separate genus.

Our robust phylogenetic reconstruction of the Fagaceae provides strong evidence of the paraphyly of subfamily Castaneoideae (Fig. 1) with major implications for our understanding of cupule evolution (Fig. 3). Support for *Chrysolepis* as the sister genus to *Lithocarpus* s.s. combines two genera that each possess well-defined cupule/fruit apomorphies. One possible synapomorphy for this relationship is the flower cupule (*sensu* Forman 1966a), where each pistillate flower in a dichasium is surrounded by cupular tissue. The placement of the new genus *Notholithocarpus* within the *Quercus* and *Castanea* + *Castanopsis* clade suggests that its single-fruited cupule is derived from reduced dichasial cupules via loss of lateral flowers (Fig. 3). Developmental data from *Quercus* indicates two initiation points or primordial cupule valves subtend the pistillate flower (MacDonald 1979), which represents a different ontogenetic process than the completely valveless cupule of *Lithocarpus* s.s. (Okamoto 1989). Further studies are needed to confirm these evolutionary patterns of cupule development inferred from our phylogenetic analysis of DNA sequence data.

Delimitation of the castaneoid genera can be difficult, as few traits are truly fixed and exclusive to a single genus. For example, while most species of *Castanea* and *Castanopsis* possess three pistillate flowers per cupule, certain species in these genera have a single pistillate flower per cupule, a trait that normally defines *Lithocarpus* s.s. (Fig. 3). A combination of traits is often needed and *Notholithocarpus* is no exception. In addition to DNA sequences and pollen morphology, other potentially diagnostic features to distinguish *Notholithocarpus* from *Lithocarpus s. s.* are foliar, namely the lack of an acuminate tip, sclerophyllous leaves bearing multiradiate trichomes (Jones 1986, see Type 10), unbranched secondary veins that extend to the margin, and the potential for serrate margins in *Notholithocarpus*, although some species of *Lithocarpus s. s.* also bear slightly toothed margins. Our studies also included a comprehensive examination of literature-based reports on inflorescence structure, morphology of staminate and pistillate flowers,
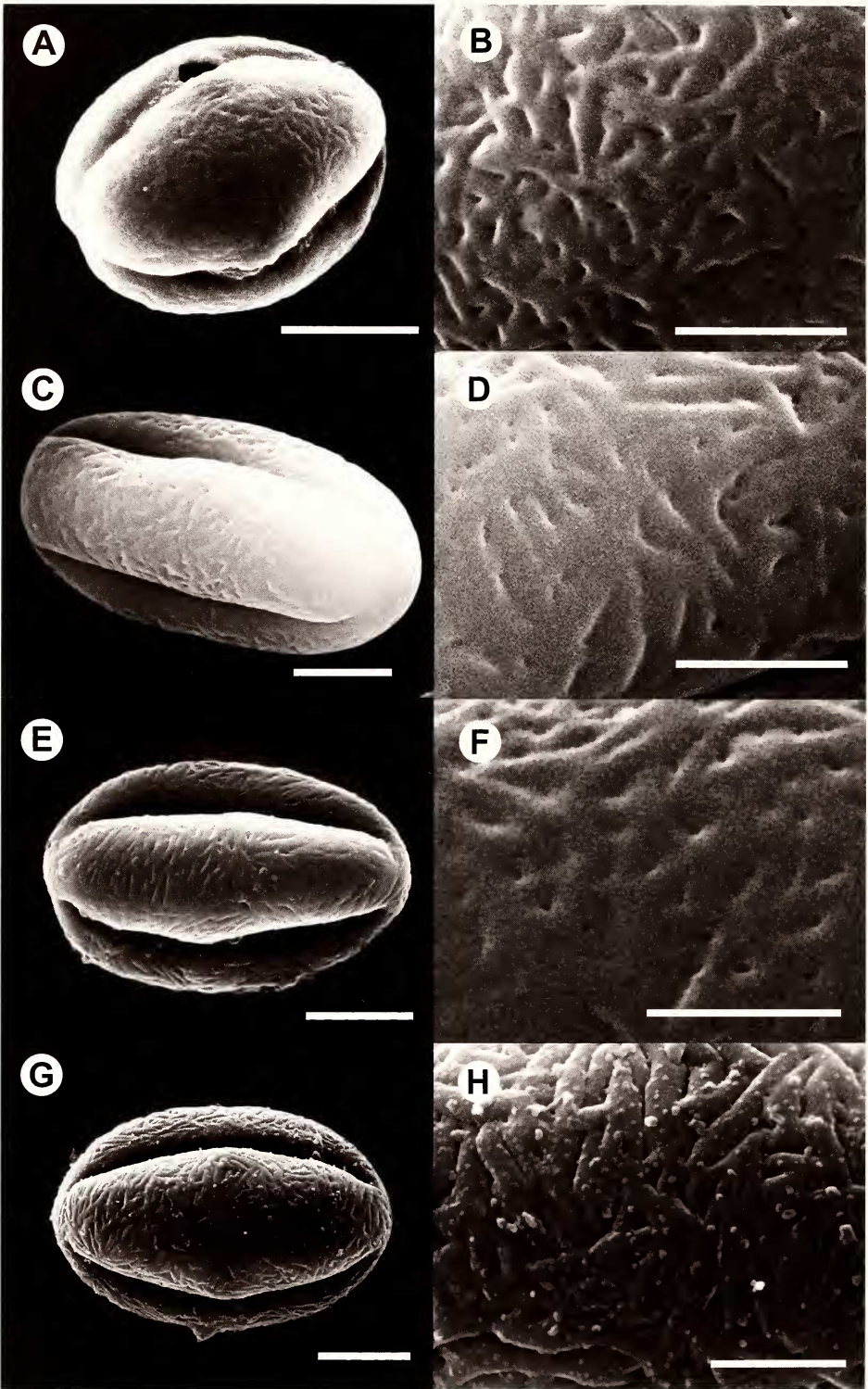
FIG. 2. Pollen of select castaneoid taxa. A & B. *Notholithocarpus densiflorus* (*Stone 3034*); C & D. *Chysolepis chrysophylla* (*I. Olmsted 259*); E & F. *Lithocarpus dealbatus* (*Manos 1288*); G & H. *Castanopsis indica* (*Manos and Zhou 1426*); Scales: A, C, E, and G = 5 μm; B, D, F, and H = 2 μm.
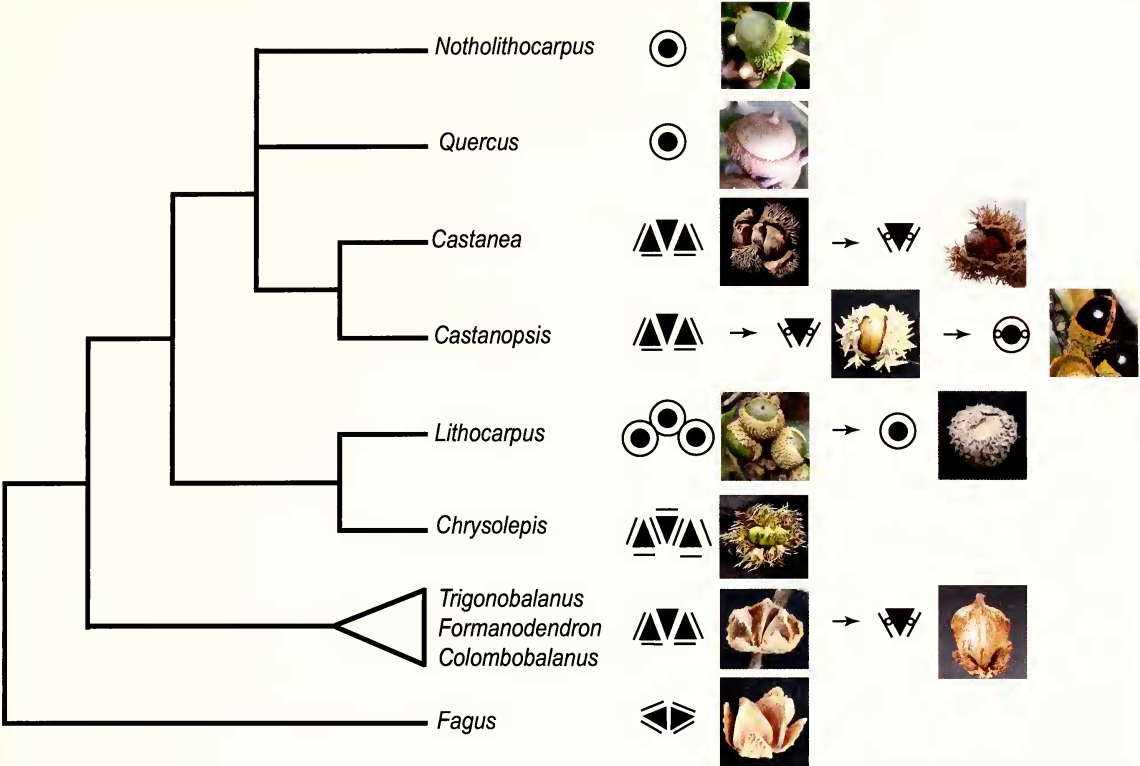
Fig. 3.   Summary of the phylogeny of Fagaceae with a set of diagrams and images of representative cupule/fruit types. Cupule valves are indicated with straight lines and valveless cupules with large circles. Fruits are drawn with discs or triangles, and aborted flower position with small circles. For example, the unifloral cupule/fruit in *Notholithocarpus* is shown with a disc in a large circle. Arrows indicate observed transformations within that clade or within the inflorescence. Photographs are taken from the following species: *Notholithocarpus densiflorus*; *Quercus coccinea*; *Castanea crenata*; *Castanopsis tribuloides* (left) and *Castanopsis fissa* (right); *Chysolepis chrysophylla*; *Lithocarpus fenestratus* (left) and *Lithocarpus rotundatus* (right); *Colombobalanus excelsa* (left) and *Formanodendron doichangensis* (right); *Fagus grandifolia*.

wood anatomy, and cupule ornamentation among castaneoids (Carlquist 1984; Kaul and Abbe 1984; Kaul 1987; also see http://insidewood.lib.ncsu.edu/search/), but no clear differences were detected in these features.

The phylogenetic position of CA-FP castaneoids as highly divergent members of two different major Fagaceae lineages reinforces the concept that these paleoendemic taxa are remnants of an ancient and formerly widespread broadleaf evergreen flora, which persists today in the Indochinese tropics. Additional evidence for this is based on the appreciable level of fossil diversity among likely thermophilic castaneoids in North America (Crepet 1989; Crepet and Daghlian 1980; Crepet and Nixon 1989a; Manchester 1994; Mindell et al. 2007). The macrofossil record also indicates the minimum divergence time between *Chrysolepis* and *Lithocarpus* s.s. to be at least 40 mya based on fossils unambiguously assigned to *Lithocarpus* s.s. (Kvacek and Walther 1989). This scenario suggests that the CA-FP castaneoids were established in the early Tertiary, which agrees with other broadleaf

evergreen taxa known to have dispersed through the North Hemisphere via Beringian and North Atlantic Land Bridges (Tiffney and Manchester 2001).

Taxonomic Treatment

Tanbark oak is a well-known element of the CA-FP and is a major focus of research into the spread of sudden oak death (SOD; Rizzo et al. 2005). Our results clarify its phylogenetic position in the Fagaceae and its affinities with temperate oaks and tropical chestnuts. The fact that it is more closely related to the victims of the devastating chestnut blight, *Castanea spp.*, than to its mistaken congenerics, the stone oaks, should provide insight into the evolutionary dynamics of fungal infection and resistance. Here, we place tanbark oak into a newly recognized genus, *Notholithocarpus*, which reflects its false or convergent similarity to Asian *Lithocarpus* s.s. We make this new combination without subfamilial designation, as further work is required to produce a valid nomenclature at that level.

Notholithocarpus Manos, Cannon & S. Oh, gen. nov. TYPE: *N. densiflorus* (Hook. & Arn.) Manos, Cannon & S. Oh.

A Lithocarpo foliis sclerophyllibus trichomatibus multiradiatis et polline subprolato (sphaeroideo) differt.

Notholithocarpus densiflorus (Hook. & Arn.) Manos, Cannon & S. Oh, comb. nov. Basionym: *Quercus densiflora* Hook. & Arn., Bot. Voy. Beechey, p. 391, 1840. TYPE: USA, California, *D. Douglas s. n.* (holotype: K!, isotype: GH!)

For intraspecific taxonomy, we follow other treatments (Tucker 1993; Nixon 1997).

Notholithocarpus densiflorus var. *densiflorus*

Notholithocarpus densiflorus var. *echinoides* (R. Br. ter) Manos, Cannon & S. Oh, comb. nov. Basionym: *Quercus echinoides* R. Br. ter, Ann. Mag. Nat. Hist., 4. 7:251. 1871. TYPE: USA, Oregon, Canon Creek, Siskiyou Mountains, *Brown 250* (Holotype K, isotype: K!).

The genus name *Pasania*, a local name for one of the species in Java (Rehder 1916), also was applied to tanbark oak by Örsted (1866). In order to preserve its usage within the synonymy of *Lithocarpus*, we designate a type for the genus name *Pasania* by using one of the species originally listed by both Miquel (1857: *Quercus* subgenus *Pasania*) and Örsted (1866: *Pasania* subgenus *Eupasania*).

Pasania (Miq.) Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, 8:81, 1866. Basionym: *Quercus* subgenus *Pasania* Miq., Fl. Ned. Ind. Vol. 1(1): 848. 1856. TYPE: *Pasania sundaica* (Blume) Oerst., (*Quercus sundaica* Blume) (lectotype designated here).

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APPENDIX I.

DNA voucher information and GenBank accession numbers for taxa used in the molecular phylogenetic study. Each entry includes species, locality, voucher specimen, and GenBank accession numbers (ITS; CRC; trnK/matK; atpB-rbcL; ndhF accession).

Castanea mollissima Blume; USA, New York, Tompkins Co., Cornell University Plantations; Manos 1038 (BH); ITS–AY040396; CRC–EU189752; trnK/matK–FJ185050; ndhF–FJ185073; Connecticut, Connecticut Agricultural Research Station; Stanford R1T15 (UNC-CH); atpB-rbcL–AY042453.

Castanopsis argyrophylla King ex Hook.f.; China, Yunnan, Menglian; Manos and Zhou 1402 (DUKE); AY040376; EU189758; FJ185051; FJ185059; FJ185074.

Castanopsis carlesii (Hemsl.) Hayata; China, Yunnan, Jingu; Manos and Zhou 1382 (DUKE); AY040372; EU189760; FJ185052; FJ185060; FJ185075.

Castanopsis fissa (Champ. ex Benth.) Rehder & E. H. Wilson; China, Yunnan, Simao; *Manos and Zhou 1396* (DUKE); AY040392; EU189763; FJ185053; FJ185061; FJ185076.

Chrysolepis chrysophylla (Douglas ex Hook.) Hjelmq.; USA, Oregon, Benton Co., St. Mary's Peak; *Manos s.n.* (DUKE); AF389087; EU189770; FJ185045; FJ185062; FJ185077.

Colombobalanus excelsa (Lozano, Hdz-C. & Henao) Nixon & Crepet; Colombia, Virolin; *Nixon 4655* (BH); AF098412; EU189772; AY042456+AY040492; FJ185063; FJ185078.

Fagus grandifolia Ehrh.; USA, New York, Tompkins Co.; *Manos 114* (BH); AY040509; EU189851; U92861+AY042400; AY042412; FJ185079.

Formanodendron doichangensis (A. Camus) Nixon & Crepet; China, Yunnan, Menglian; *Manos and Zhou 1400* (DUKE); AY040452; EU189773; FJ185046; FJ185064; FJ185080.

Lithocarpus pachylepis A. Camus; China, Yunnan, Da Wei Shan; *Manos and Zhou 1451* (DUKE); AY040441; EU189792; FJ185054; FJ185065; FJ185082.

Lithocarpus xylocarpus (Kurz) Markgr.; China, Yunnan, Da Wei Shan; *Manos and Zhou 1463* (DUKE); AY040426; EU189801; FJ185055; FJ185066; FJ185083.

Notholithocarpus densiflorus var. *echinoides* (R. Br. ter) Manos & S. Oh (*Lithocarpus densiflorus* var. *echinoides* (R. Br.) Abrams); USA; California, Nevada Co., Washington; *Manos and Tucker 922* (BH); AY040370, EU189783; FJ185047; FJ185067; FJ185081.

Quercus myrsinifolia Blume; USA, Georgia, USDA Coastal Research Station. Savannah; *Manos s.n.* (BH); ITS–AF098414; California, Yolo Co., Shields Grove Arboretum; no voucher; *CRC*–EU189824; *trnK/matK*– FJ185048; *atpB-rbcL*– FJ185068; *ndhF*– FJ185084.

Quercus robur L.; USA, New York, Tompkins Co., Cornell Univ. Campus; *Manos s.n.* (BH); AF098424; EU189832; FJ185056; AY042505; FJ185085.

Quercus rubra L.; USA, New York, Tompkins Co., Cornell Univ. Campus; *Manos s.n.* (BH); AF098418; EU189836; FJ185057; FJ185069; not determined.

Quercus suber L.; USA, California, Santa Barbara Co., Orella St.; *Manos 423* (BH); AF098434; EU189843; FJ185049; FJ185070; FJ185086.

Quercus tomentella Engelm. USA, California. Santa Barbara Co. Santa Cruz Island; *Manos 983* (BH); AF098437; EU189845; FJ185058; FJ185071; FJ185087.

Trigonobalanus verticillata Forman; U.K., Scotland, Edinburgh, Royal Botanical Gardens; *RBG 1967-421*; AF098413; EU189847; U92866+AY042455; FJ185072; FJ185088.